

17 Population Trends and Limiting Factors in *Boiga irregularis*

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An incipient animal population is likely to undergo an initial period of exponential growth, followed by a period with a less predictable outcome (Gray et al., 1986; Groves and Burdon, 1986; Mooney and Drake, 1986; Drake et al., 1989; Hengeveld, 1989). If ecological feedback loops are short and the introduced species can coexist with the resident species, the invader's numbers may approach carrying capacity slowly and then stabilize, with no radical changes in community structure. On the other hand, if feedback loops are long or coexistence is not possible, a period of chaotic changes in the community may ensue. Entire populations may be extirpated, with each loss of a member species further disturbing the community's equilibrium. In the case of the introduced Brown Treesnake (*Boiga irregularis*) on Guam, we are now witnessing a period of extreme instability. Documentation of the community changes may help us understand the ecological forces that direct and constrain the responses of predator and prey. Understanding these forces is necessary for wise management, both on Guam and on any other islands the snake may reach.

After the degree of the snake's impact on Guam's avifauna was recognized in the mid-1980s, systematic demographic studies of snake populations were initiated. The size structure of a sampled population on Guam suggested high recruitment and dense populations in recently colonized areas (Fritts and Scott, 1985). Throughout Guam, the Brown Treesnake population showed sexual size dimorphism, differences in population composition, and variation in densities between urban and rural sites and between northern and southern areas (Savidge, 1991). Body size distributions in Australia were similar in shape to those on Guam, but suggested smaller maximal sizes (Shine, 1991a). The evidence of how the snake arrived on Guam and some of the changes in population density through 1990 were summarized by Rodda et al. (1992). The population sampling techniques used and their limitations were reviewed by Rodda and Fritts (1992a). In this chapter we review the available data on the densities and composition of the Guam snake population, compare the vertebrate community on Guam with those on snake-free oceanic islands and six localities in the snake's native range,

and discuss population limiting factors that may guide control of extralimital populations.

MATERIALS AND METHODS

The techniques used for the analysis of historical trends (before 1985) in Brown Treesnake communities are given in Rodda et al., 1992. Native birds are no longer an important food for Brown Treesnakes on Guam (Savidge, 1988). Thus, to analyze the recent community dynamics affecting the Brown Treesnake, we have concentrated on quantifying populations of the snake and its mammalian and reptilian predators, competitors, and currently available prey. We quantified nocturnal species by time-constrained (>1500 person-hours) or distance-constrained (>600 km) visual searches (Rodda and Fritts, 1992a). We augmented the visual counts with snap-trap sampling of rats (>1200 trap-nights). Diurnal lizards were sampled using adhesive traps (>31,000 trap-hours; Rodda et al., 1993). In addition to using visual surveys for relative counts of Brown Treesnakes, we estimated absolute population sizes from six mark-recapture studies (Rodda and Fritts, 1992a). Not all techniques were applied to all sites. We used one or more techniques on at least 61 sites on Guam, 67 sites on snake-free islands of the Marianas, and 35 sites in the Brown Treesnake's native range (Papua New Guinea and the Solomon Islands).

Snakes that were to be released were first held to a tape and stretched with light pressure until they could be measured when momentarily relaxed. They were sexed using a very thin sexing probe (see Jordan and Rodda, 1994, for validation of technique). Snakes not released were measured without stretching (relaxed after death by anesthesia), weighed, and then sexed. In paired measurements of 22 snakes measured both before and after death, the lengths taken from live specimens averaged 104.5% ($SD = 1.4\%$) of the lengths taken from dead but unstretched snakes.

The mathematical analysis of mark-recapture data is well developed (Otis et al., 1978; White et al., 1982; Pollock et al., 1990; Lebreton et al., 1992), but the available methods are ill-suited to the demographics of snakes (Parker and Plummer, 1987). Under most conditions, snakes tend to be rarely seen and difficult to capture, and capture numbers often exhibit high coefficients of variability. In the following discussion, N represents population size and p expresses the percentage of the population caught on a given capture occasion. In our experience, snake populations that are compact enough for study generally have $N < 50$ and $p < 0.10$. White et al. (1982: 165), argued that "if $N < 100$ and $p < 0.35$, no capture-recapture experiments will provide unbiased and precise estimates." An additional concern is that the sampled area is often contiguous with areas of nonsampled snakes (the population is "open"). Because the movements of individual snakes are poorly understood, it is often difficult to discern the boundary between sampled and nonsampled areas.

Estimating snake densities is a two-sided problem. One must establish the number of snakes in a population (abundance) as well as estimate the size of the area from which the sampled snakes were drawn (abundance/area = density). We arrived at two possible solutions to the problem of estimating abundance. The computer program SURGE (Lebreton et al., 1992) has excellent algorithms for estimating p using open population models, although SURGE does not estimate population size. If SURGE fails to find temporal variability in p , it is probably reasonable to assume that the population size in a study area is in dynamic equilibrium and that the average capture probability (\hat{p}) is well estimated by SURGE. For the same period of time, the mean number of captures, \bar{n} , is tabulated (not estimated). \hat{N} , the estimated total population size, is given by the relationship $\hat{N} = \bar{n}/\hat{p}$ (Pollock et al., 1990). This approach produces results that are consistent with the trend of the population estimations of closed population models (program CAPTURE, White et al., 1982) over intervals of 20, 15, 10, and 5 days projected to the X-intercept. The advantage of using SURGE is that the full amount of information in the 20+ day sample can be utilized, yielding greater precision.

The problem of estimating the size of the area sampled is harder to solve. The CAPTURE program has an algorithm for estimating the size of the area sampled, but this closed-population model is inappropriate for the rapid population turnover of Brown Treesnakes, and the algorithm relies on small subsets of the traps for abundance estimates of subsets of the population. In our experience, the confidence intervals for these small subsets are too large for usable extrapolation with snakes. Instead, we estimated the sampling area by comparing the capture rates of central versus peripheral traps (Fig. 17.1). We assumed the average central trap captured snakes from its sector of the trapping grid, but the peripheral traps had more captures because their sample included areas beyond the nominal grid boundary (i.e., the outer area for which they were not competing with other traps for captures). If the trap spacing is 15 m (as in Fig. 17.1), the average central trap samples 225 m². One can estimate the size of the peripheral area sampled by multiplying the product of this number and the number of peripheral traps by the ratio of average captures for peripheral traps/average captures of central traps. An equivalent approach is to assume that all traps sample 225 m² and reduce the estimated total population size by the fraction of captures represented by excess captures in the peripheral traps. In our studies, only a modest percentage (10–20%) of total captures were “excess” captures of the peripheral traps (Fig. 17.1).

RESULTS AND DISCUSSION

Population Density

The Brown Treesnake population on Guam originated in the immediate post-World War II period. Population growth and expansion were continuous but not necessarily steady from 1950 to 1980 (Rodda et al., 1992). When snake pop-

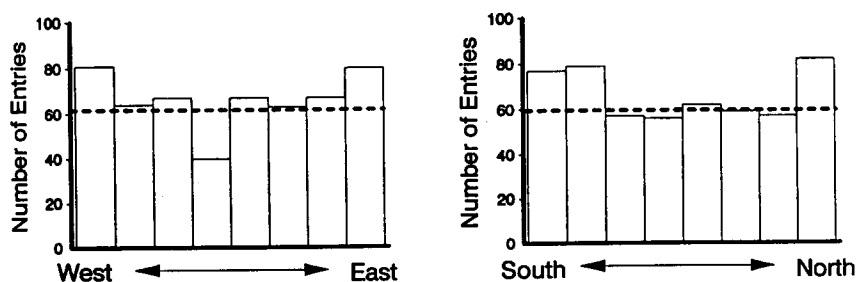


Figure 17.1 Row and column totals for Orote Point trap grid, 1991. Dashed lines show means for interior traps and give a graphical indication of the "excess" captures in the peripheral traps. The procedure for computation of means for central versus peripheral traps is described in the text.

ulations were first quantified in 1985, an especially dense population of snakes at a site in northern Guam was estimated at 80–120 snakes/ha. This probably represented the initial irruption peak for snakes at that northern site. Rodda et al. (1992) used CAPTURE, which assumes a closed population, to compute this density, perhaps overstating the real population size. Using improved open population analysis we recomputed the estimations from the raw data and found that a modest downward revision is warranted. Although insufficient data exist to put firm confidence intervals on the original estimates, subsequent measurements of comparable areas suggest that 50–100 snakes/ha were probably present in selected localities at the peak of the initial irruption. This range is still high for large snakes away from water or dens (Fig. 17.2).

With the large numbers of captures (145–345 in 1.5 months) made possible with mouse-attractant snake traps (Rodda et al., this volume, Chap. 20) and the improved computational methods described above, we estimate recent densities of snakes at Orote Point, Guam, at 49/ha (95% confidence limits 36–73) in 1990, and 37/ha (27–54) in 1991, and 24/ha (13–49) at a Northwest Field site in 1992. The Orote site is near the location of Guam's initial colonization and has probably had snakes for several decades. The lower density at the Northwest Field site is consistent with the declining population in northern Guam noted by Rodda et al. (1992). It may reflect a failure of the prey community to recover from the high snake population of 1985. The existence of a dense snake population at Orote, in an area long colonized, suggests that Brown Treesnakes will continue to occur, at least episodically, at high densities.

In addition to these absolute population estimates, we have visual sighting rates for about 60 sites on Guam. These indicate that populations in many areas change dramatically from year to year, often with no obvious general trend. Adjacent areas sometimes follow contrary trajectories. Areas of the same forest type often do not exhibit similar sighting rates. These inconsistencies suggest that factors other than

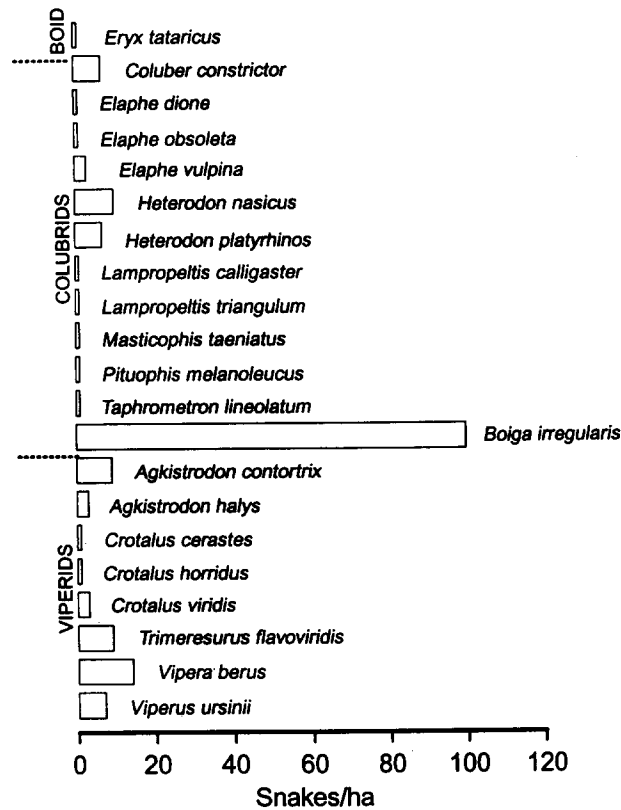


Figure 17.2
Maximum reported
densities of large
snakes away from
water or dens
(non-*Boiga* values
from Parker and
Plummer, 1987).

habitat structure are important in determining the abundance of the snake. We are collecting data to test the hypothesis that prey abundances and an area's history of predator-prey interactions are the key determinants of population density.

The densities of snakes continue to be higher than the maximum reported densities for all avian prey species at their most favorable sites (26.1 birds/ha: Engbring and Ramsey, 1984). To date, the only directly observed predation on a wild native bird by a Brown Treesnake was a snake with a snout-vent length (SVL) of 785 mm consuming an egg of a Mariana Crow (*Corvus kubaryi*), Guam's largest passerine. Thus, all but the youngest hatchling snakes should be capable of eating eggs of the smaller birds (Chiszar, 1990). When given the opportunity, Brown Treesnakes can sustain a dietary intake of at least 40% of their body mass per month (Collins and Rodda, 1994). Based on the weights of snakes captured in our surveys, a high-density Brown Treesnake population on Guam has an aggregate mass of 3–5 kg/ha. Thus the snakes in a hectare could potentially eat 1.2–2.0 kg prey/month, or 14–24 kg/year. Unfortunately, average weights are not available for many of Guam's birds. Micronesian Honeyeaters (*Myzomela saffordi*) averaged

13.3 g (Jenkins, 1983); at the other extreme are Guam Rails (*Rallus owstoni*), males of which averaged 241 g (Jenkins, 1979). We interpolated among these, guided by the birds' known lengths (Jenkins, 1983) and the masses of North American birds of similar lengths (Dunning, 1984). The estimated mass of each species multiplied by the number of each species at the maximum reported density yields a total bird mass of around 0.8 kg/ha. Therefore, a dense population of Brown Treesnakes on Guam has the capacity to consume annually about 18–30 times the biomass of adult birds that were present under the most favorable conditions.

Size Structure

Savidge (1991) showed that large Brown Treesnakes on Guam in the early 1980s were more conspicuous in urban areas and in southern Guam. Southern Guam has extensive savanna habitat, and rats are relatively abundant there (Barbehenn, 1974; Savidge, 1986). Urban areas tend to have more commensal endotherms, especially rats and chickens, and snakes are more likely to be found in association with these. Compared with forests, where the native endotherms have been extirpated, savannas and urban areas have a relatively rich food base for large snakes. Thus it is not surprising that large snakes are more common in these areas (Fig. 17.3; Savidge, 1991). Large snakes are overwhelmingly male (Fig. 17.3; McCoid, 1990; Savidge, 1991).

The evolutionary and proximate causes of the large sexual size dimorphism present in the Guam population are not evident. Sexual size dimorphism may occur because one sex terminates growth earlier than the other, one sex grows more rapidly than the other, or one sex enjoys lower mortality than the other. We have no evidence with regard to the duration of growth in Brown Treesnakes. Rodda et al. (this volume, Chap. 2) cited evidence for a less variable but not higher growth rate in maturing males. Some evidence for greater female mortality comes from comparing the size distributions of captive and wild-caught snakes (Fig. 17.3). The captive males exhibit sizes in the range of wild conspecifics, whereas the largest captive females greatly exceed the size of the largest wild females. Captive females differ from their wild counterparts in having ample food but, in this case, no opportunity to breed. We have no evidence to refute the possibility that the denial of breeding opportunities redirects growth into somatic channels in captive females only, but breeding activities may also result in higher energy stress and therefore greater mortality in the wild females. Some support for this position comes from the work of Jordan and Rodda (1994), who found that recent samples of adults from Guam were more male biased in sex ratio than earlier samples and that adult females had sharply deteriorated in their mass-to-length ratio, suggesting physiological stress. The extirpation of native endotherms, the primary food of adult Brown Treesnakes (Greene, 1989), may have produced a food shortage more acutely felt by reproductive females. The Brown Treesnakes Nichols (in litt., 1992) examined on Guam were unusually low in fat reserves, suggesting food stress.

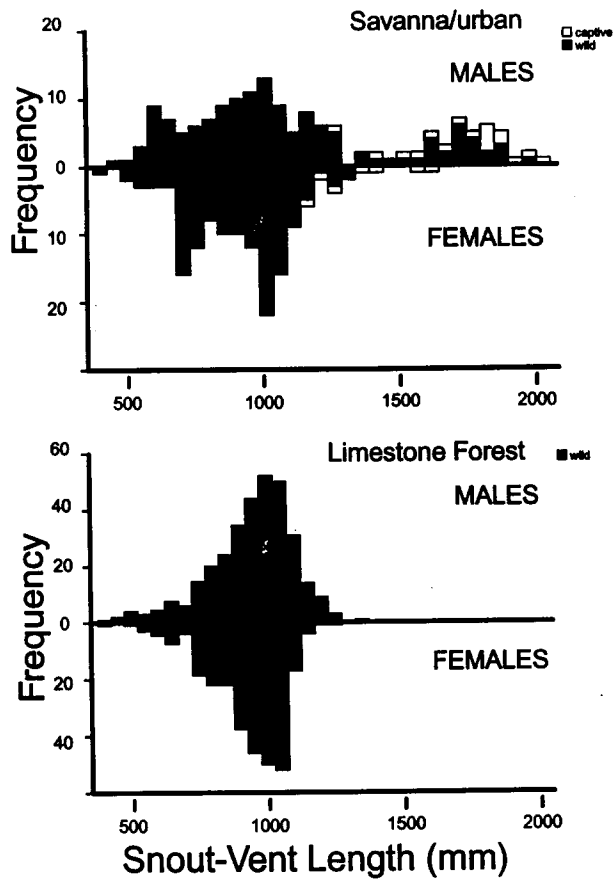


Figure 17.3 Size histogram of snakes from Guam and captivity (captive values from D. Chiszar, pers. comm., 1993). Savanna and urban areas are grouped because they have a relatively rich supply of endotherm prey, especially rats and domestic fowl.

Sexual size dimorphism is not unique to Brown Treesnakes on Guam, however. We found it to be present in specimens from Papua New Guinea and the Solomon Islands, and Shine (1991a) recorded it for Australia. A leading evolutionary argument for male-biased sexual size dimorphism in snakes is that large males enjoy a mating advantage (Shine, 1978). This would occur if females preferred to mate with larger males, or if larger males were better able to exclude smaller males from breeding opportunities. The latter is believed to occur in a variety of venomous snakes, and in those species "combat dances" between males are observed relatively often. We have observed several thousand Brown Treesnakes, but we have not seen behavior suggestive of "combat dances." Nor has this behavior been reported in other parts of the range. A wildlife conservation officer on Guam reported a brief encounter between two male snakes that involved the larger snake pushing downward on the smaller snake (McCoid, pers. comm., 1989), but this observation is more notable for its uniqueness than for its conclusiveness. We have found no evidence for intermale avoidance in small

aggregations of snakes found in traps or natural crevices (Rodda et al., this volume, Chap. 2).

The other leading hypothesis for the evolution of sexual size dimorphism is that of feeding niche specialization between the sexes (Camilleri and Shine, 1990). Dietary studies in Australia (Shine, 1991a), Guam (Savidge, 1988), and non-Australia parts of the native range (Greene, 1989) emphasize the breadth rather than the specialization of *Boiga* diets. Shine (1991a) explicitly rejected a sexual difference in diet. If the fairly extreme sexual size dimorphism of Brown Treesnakes has an evolutionary basis, the selective forces responsible have yet to be identified.

Sex Ratio

Skewed sex ratios may be the result of differential mortality or differential catchability. Collections of juvenile Brown Treesnakes rarely differ significantly from a 1:1 ratio, but samples of adults are usually male biased in Guam (Savidge, 1988) and Australia (Shine, 1991a). This could be due to greater male catchability, greater male survivorship, different growth trajectories, or a combination of these. As Rodda et al. noted in Chapter 2 of this volume, gravid females are rarely collected. We have too few data to determine if the paucity of gravid females is responsible for all of the difference between the sexes in capture frequencies. It could account for some of the sex ratio differences between sites (Fig. 17.4), but a small shift among areas in the fraction of adult females that are gravid would not likely produce the radical changes in sex ratio among sites shown in Figure 17.4. Note that the sex ratio differences among sites are more pronounced than are those among habitats (Fig. 17.4). When sites are pooled (e.g., Andersen Air Force Base, North Guam, and habitat comparisons in Fig. 17.4), sex ratio differences tend to be muted and stable over time. The significant differences tend to occur in single sites rather than broad areas. Savidge (1991) suggested greater mobility of males to explain a preponderance of males in an area more recently colonized. Movements might also account for some of the other local sex ratio differences, but direct documentation and evidence for the proximate causes of the movements are lacking.

Mature Fraction

The average size at maturity appears to vary among different parts of the Brown Treesnake's range (Greene, 1989; Shine, 1991a; Rodda et al., this volume, Chap. 2). We based our estimate of mature fraction on size distributions relative to the applicable local criterion for size at maturity (Rodda et al., this volume, Chap. 2).

Mature snakes are relatively uncommon on Guam (Fig. 17.5). The mature fraction is low not only in contrast to samples from the native range (Fig. 17.5), but also in relation to other nonvenomous snakes (Fig. 17.6). The contrast is sharper

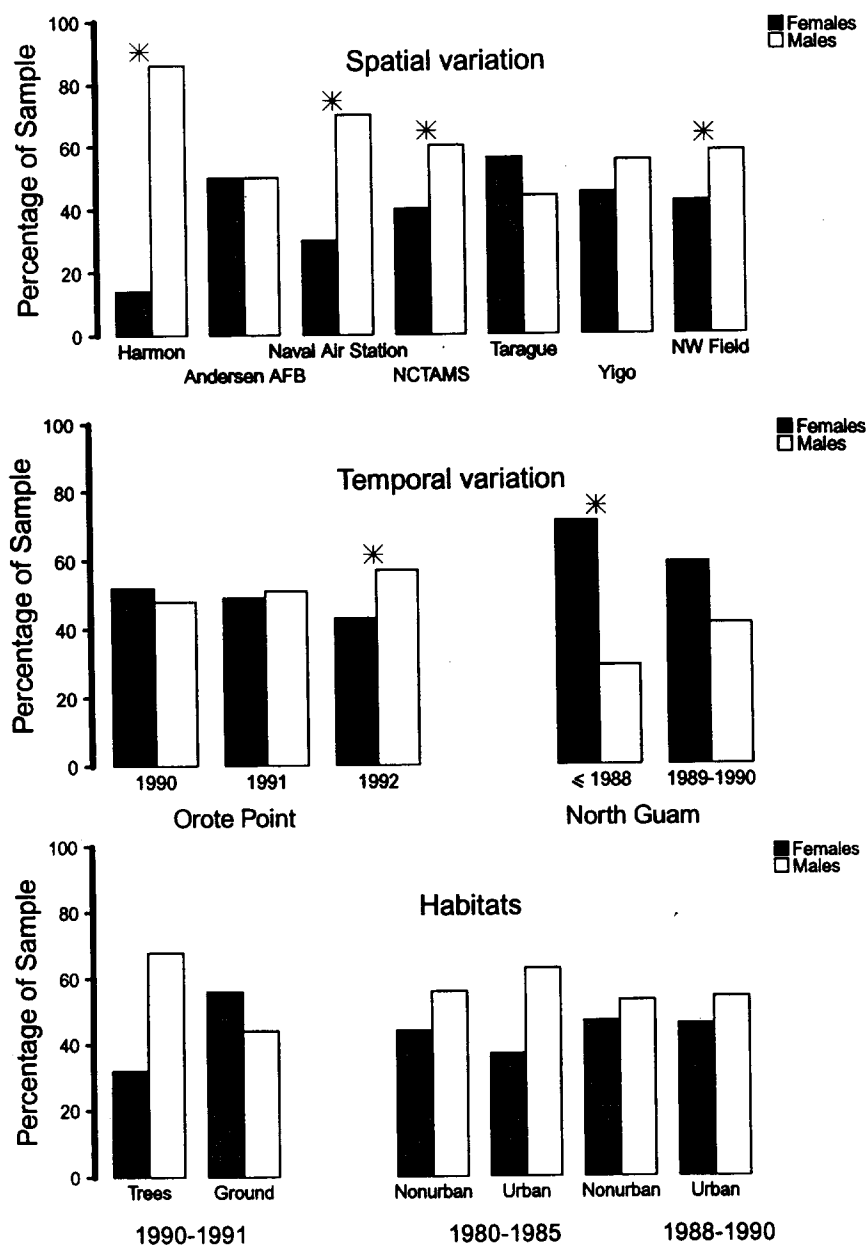


Figure 17.4 Sex ratios from a variety of sites in Guam. Asterisks indicate samples whose counts deviate significantly from 1:1 ($\alpha < 0.05$; G test with Williams correction). (North Guam data are from Jordan and Rodda, 1994; 1980-1985 data are from Savidge, 1991.)

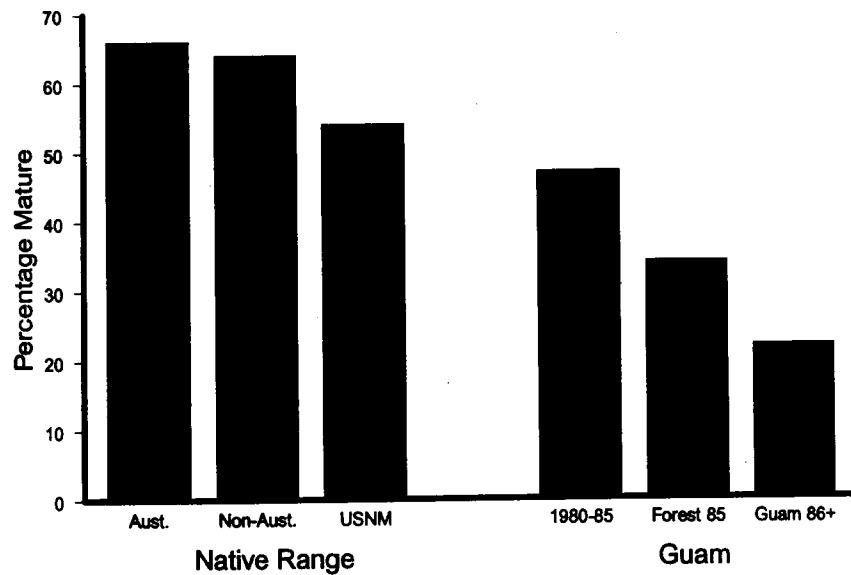


Figure 17.5 Percentage of mature Brown Treesnakes in samples collected from Guam and the native range. (Australia data from Shine, 1991; non-Australia data from Greene, 1989; U.S. National Museum [USNM] data are mostly from the islands north of Papua New Guinea [Admiralty and Bismarck Archipelagos].)

than that suggested by Figure 17.6, however, as low mature fractions are associated with high-fecundity species (Fig. 17.7), and *B. irregularis* is a species with low fecundity.

The anomalous position of current Brown Treesnake populations on Guam may be due to an unusually large number of small snakes, a dearth of large snakes, or both. In the following section we present some data suggesting that food for juvenile snakes is more abundant on Guam than it is in the native range. The greater abundance of food might enhance juvenile survivorship and produce relatively high numbers of juveniles on Guam. In contrast, the recent extirpation of most native endotherms appears to have reduced the prey supply for large snakes on Guam, perhaps increasing adult mortality and reducing the abundance of mature snakes.

Limiting Factors

It is an article of faith among many policy makers that the high abundance of Brown Treesnakes on Guam is due to the absence of some predator that suppresses populations of the snake in its native range. Although *Boiga* has competitors throughout its native range, we have been unable to identify any predators in the

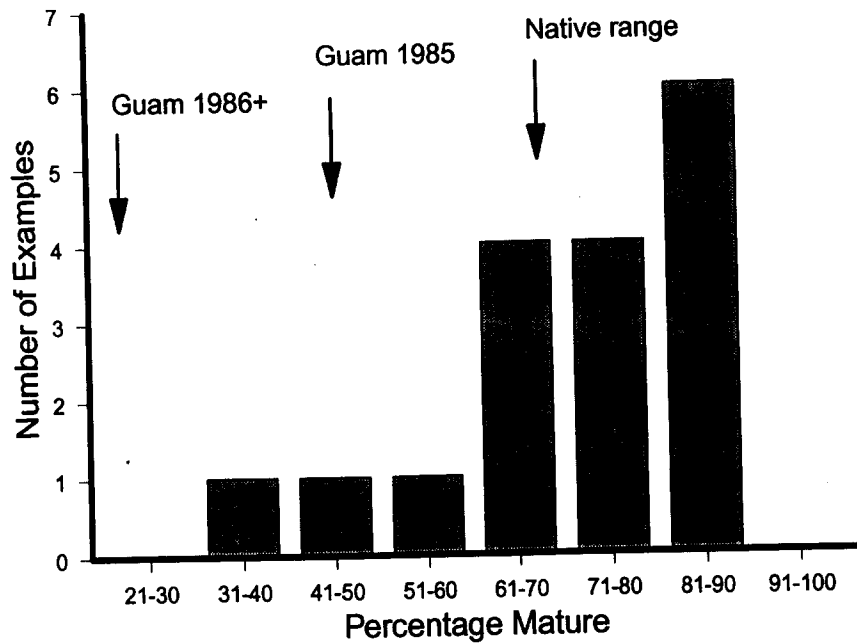


Figure 17.6 Percentages of mature snakes in samples of nonvenomous snakes reported by Parker and Plummer (1987). Each species is represented once, by the average of the available data. The arrows show values for single venues of *B. irregularis*.

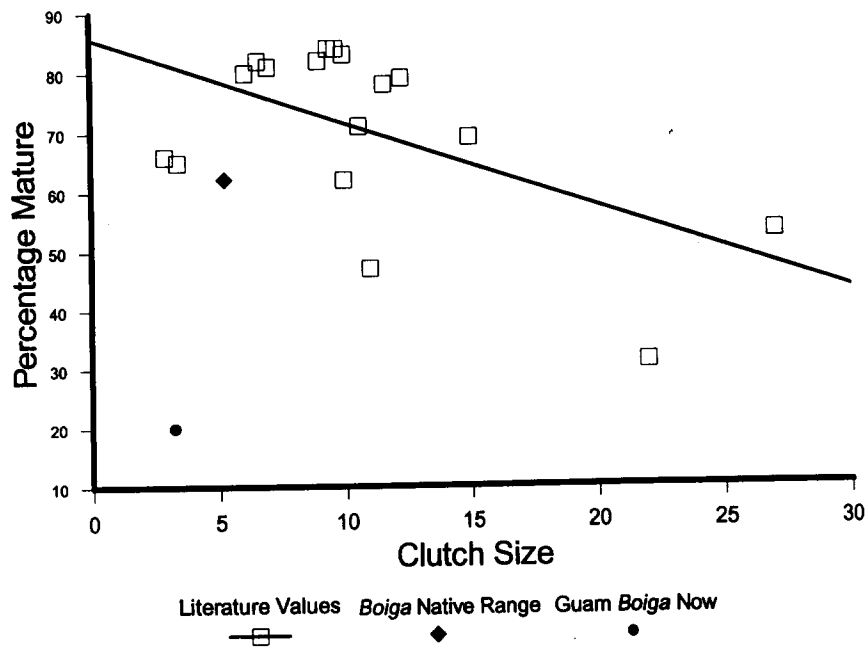


Figure 17.7 Maturity in relation to fecundity. (Clutch or litter size averages from Seigel and Ford, 1987.)

eastern end of its range. On Malaita, Solomon Islands, for example, there are no carnivorous mammals, no snake-eating birds, and, with one exception, no reptiles that eat Brown Treesnake adults or eggs. The one exception, *Varanus indicus*, is also present on Guam, where it apparently does not hold down snake numbers. Humans on Malaita do not eat Brown Treesnakes. The vegetation on Malaita (a mix of gardens and old- and second-growth forests) is similar to that on Guam and seems ideal for the snake. Yet, our average sighting rate for Brown Treesnakes on Malaita was 0.10/h, about 5% of the average for the same searchers on Guam. From this and other examples we conclude that neither predation nor habitat structure is the primary factor limiting populations of Brown Treesnakes in many areas. Shine (1991b) reached a similar conclusion for Australian elapids.

On one occasion we saw a Brown Treesnake attempt to eat a conspecific. In this case the snake being eaten was larger; consummation of the feeding attempt was interrupted and may not have been possible. There are frequent opportunities for Brown Treesnakes to eat smaller conspecifics, and the absence of other reports (through direct observation or analysis of the contents of the 1500+ stomachs that have been examined) suggests that cannibalism is not an important ecological pressure on Brown Treesnake populations.

Are competitors limiting the snake? Competition may be either direct (interference competition) or indirect (depletion of shared resources). We know of no evidence to suggest that any organism directly interferes with foraging Brown Treesnakes, but there is evidence that prey availability is lower in the native range than it is on Guam or nearby snake-free islands (Fig. 17.8). This is consistent with a role for either competition or simple food shortage (i.e., not attributable to competitors). Figure 17.8 shows the abundances of the primary foods for small and medium-sized *Boiga*. Our data on endothermic prey were too sparse for a comparable analysis of food for large snakes. With larger prey species, the vulnerability of the prey to the snake is probably as important as the number of prey present. In the absence of coevolutionary experience with snakes, the birds of Guam were probably highly vulnerable to the snake (Savidge, 1986). Adult endotherms in the native range do not appear to be nearly as vulnerable.

We constructed a stepwise multiple regression model to explore the independent contributions of the abundances of frogs, skinks, geckos, and snakes other than *Boiga* to the abundances of *Boiga* that we documented in 11 sites (6 native range, 5 Guam). Day-active lizard abundances were expressed in captures per trap-day (adhesive traps). The other rates were sightings per hour. All variables were natural $\log(n + 1)$ transformed. Using several different selection criteria, the best model was one that omitted frog abundances but included the other variables (Table 17.1). The best model explained 83% of the variance, indicating that any omitted variables were relatively unimportant ($R = 0.91$; $F = 24.27$; $df = 3, 7$; $P = 0.0004$). Note that a negative parameter value is associated with abundances of non-*Boiga* snakes; this is consistent with indirect competition for food (probably reflecting the endothermic prey we were unable to quantify directly). In the

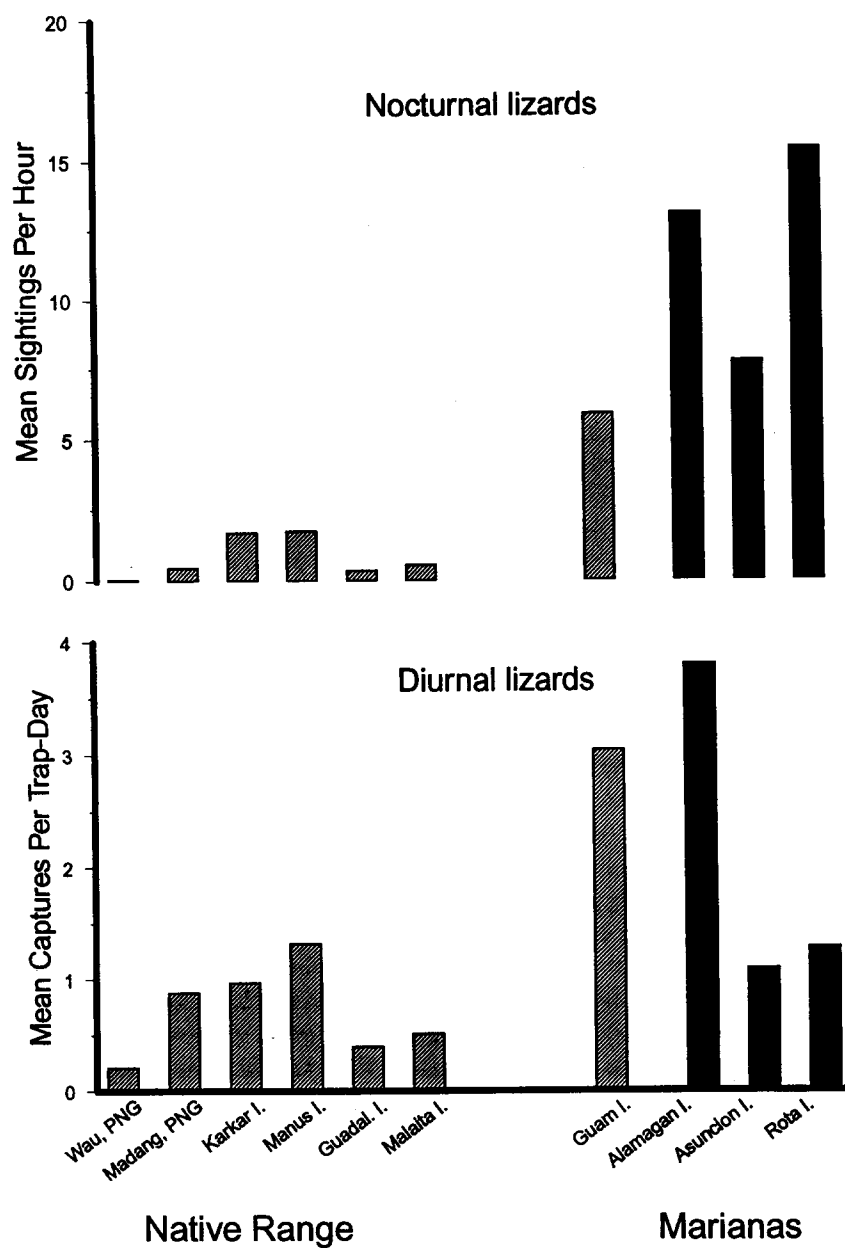


Figure 17.8 Relative abundances of diurnal (mostly skinks) and nocturnal (mostly geckos) lizards at selected sites in Papua New Guinea (PNG), Solomon Islands, and the Mariana Islands. Islands lacking snakes are represented with dark bars.

Table 17.1 Multiple regression model for the dependent variable *Boiga* sightings per hour.

Predictor variable	Parameter estimate	Standard error	Type II sum of squares	F	Probability
Skinks	0.1996	0.078	0.2373	6.69	0.036
Other snakes	-1.7264	0.676	0.2316	6.53	0.038
Geckos	0.5457	0.147	0.4827	13.61	0.0078

absence of information on nonfood variables, the model suggests that prey abundance is the most important ecological variable limiting the abundance of the Brown Treesnake.

Using the multiple regression equation, we estimated suitabilities for Brown Treesnakes of various sites in the native range and Marianas (Fig. 17.9). The composite environmental suitability index indicates that Guam and Mariana Island sites have a high suitability for the Brown Treesnake. The success of the Brown Treesnake on Guam probably derives from the abundance of food there. Based on this estimation of environmental suitability, we predict the snake will do well on Saipan and other presently snake-free islands of the Marianas if it should become established there.

The data that we used to quantify the abundances of snake food on Guam (for Fig. 17.9) were collected in 1988–1990, after the demise of most of the native forest vertebrates. However, Guam sites broadly overlap the suitability ranges of the presently snake-free sites of the Marianas, where the native vertebrates are relatively intact. This persisting high suitability of Guam sites is attributable to the success on Guam of introduced prey species, especially the house gecko *Hemidactylus frenatus* and the terrestrial skink *Carlia* cf. *fusca*. Other important food items are introduced birds, especially chickens (*Gallus gallus*), francolins (*Francolinus francolinus*), drongos (*Dicrurus macrocercus*), sparrows (*Passer montanus*), pigeons (*Columba livia*), turtle doves (*Streptopelia bitorquata*), rats (*Rattus tanezumi* and *R. norvegicus*), and native lizards (*Emoia caeruleocauda*, *Lepidodactylus lugubris*, and *Gehyra mutilata*). The native lizards that have survived are very small and have high reproductive rates (McCoid, 1989; Rodda and Fritts, 1992b). The introduction and high populations of rats on Guam before the arrival of *Boiga* and the irruptions of shrews (*Suncus murinus*) after 1952 and skinks (*Carlia* cf. *fusca*) after 1960 undoubtedly accelerated the snake's population expansion. The succession of these and other introductions must be considered in evaluating the snake populations that developed on Guam. Were it not for the highly successful introduced prey species, Guam would probably not now have a dense population of Brown Treesnakes (McCoid, this volume, Chap. 37).

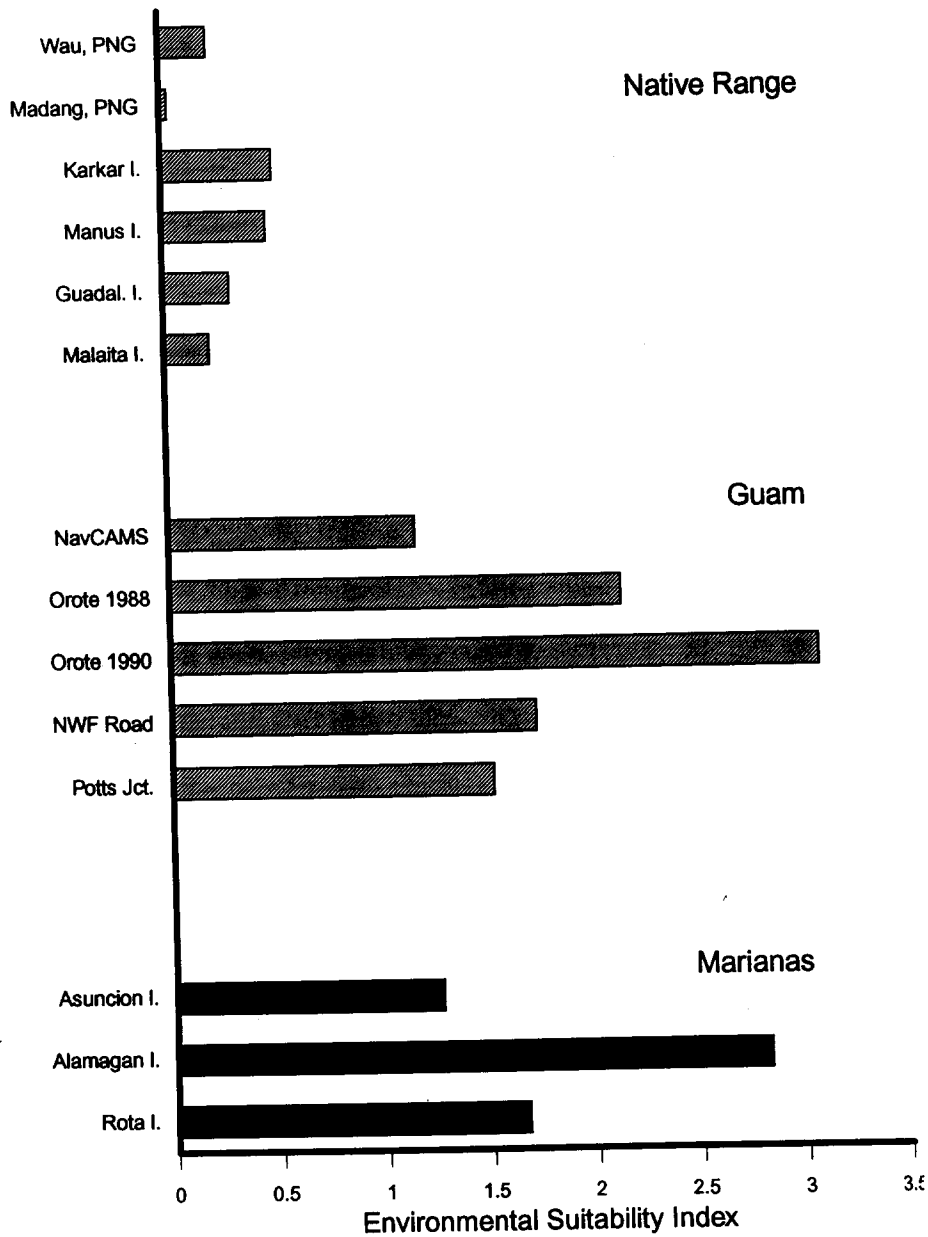


Figure 17.9 Environmental suitability of various sites in Papua New Guinea, the Solomon Islands, and the Mariana Islands. The index is based on the factors and weightings obtained from the multiple regression model in Table 17.1. Islands lacking snakes are represented with dark bars.

MANAGEMENT RECOMMENDATIONS

In the early 1990s, Brown Treesnakes continued to attain high densities in areas long colonized on Guam. Snakes will probably continue to exert significant predation pressure in some areas after the initial irruption has passed. The adverse impacts of high snake densities (Rodda et al., this volume, Chap. 2; Fritts and Chiszar, this volume, Chap. 4; Fritts and McCoid, this volume, Chap. 6) and frequent opportunities for accidental transport to other islands (Fritts et al., this volume, Chap. 14) are likely to continue.

The changing sex ratios, mature fraction, and size distributions indicate a population that is experiencing unusual local population changes. These aspects should be explored further for the management opportunities they may present. Adult females seem to be especially vulnerable to stress. If confirmed, and if augmentation of the stress were practical, it might be possible to bring about significant reductions in the number of reproductive females or their reproductive output.

Basic information is lacking regarding snake age, conditions necessary for reproduction, location of eggs, average clutch size on Guam, frequency of reproduction, and survivorship schedules. Documentation of these demographic parameters is a necessary precursor of intelligent management planning.

The introduction of snake predators will not replicate the limiting factors that constrain Brown Treesnake populations in the snake's native range. Other rationales for biological control agents should be evaluated in light of other island experiences (Howarth, this volume, Chap. 32).

Care should be taken to ensure that measures taken to make an environment inhospitable to Brown Treesnakes do not inadvertently create conditions favorable to prey species. For example, the use of bright lights to repel the nocturnal snake could incidentally increase the abundance of geckos (Petren et al., 1993), thereby indirectly increasing the attractiveness of the site for foraging snakes.

Control of the introduced species that are prey for the Brown Treesnake (pigeons, sparrows, rats, *Carlia* cf. *fusca*) should be considered in sites where it is practical (ports, airports, homes). Reducing prey abundance would be likely to limit snake numbers, although more study is needed to determine what size prey-reduced zone would be needed to redirect a significant number of Brown Treesnakes to other areas. Study of the unintended consequences of such manipulations may also be warranted.

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